

Biogeography of *Lysipomia* (Campanulaceae), a high elevation endemic: an illustration of species richness at the Huancabamba Depression, Peru

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Abstract

The genus *Lysipomia* Kunth comprises about forty species restricted to the Andean páramo and wet puna. The greatest endemism and species diversity occurs between 2°-5° S latitude (18 spp.) and 6°-8° S latitude (12 spp.) on both sides of the Huancabamba Depression. This study details the biogeography of *Lysipomia* by using cladistic analyses of morphology and nuclear DNA. Two subgenera are recognized based upon the size and color of the corolla. Area cladograms suggest that the species with large flowers and nectar guides (subgenus *Rhizocephalum*) originated in southern Peru or Bolivia and adaptive radiation has been from south to north of the Huancabamba Depression. The Depression appears to have been a significant barrier that the large corolla taxa have not been able to cross and movement appears to be in one direction only. The species with small flowers and no nectar guides (subgenus *Lysipomia*) do not show an obvious trend in adaptive radiation with respect to the Huancabamba Depression. Because most of the species occur south of the Depression, the origin of the small-flowered subgenus may have been in the mountains south of the Huancabamba Depression where the Rio Marañón has been an effective barrier separating sister species. Tests of allopatric speciation models within *Lysipomia* are incomplete but suggest that the large-flowered subgenus may have evolved sympatrically or considerable migration has occurred, whereas the small-flowered subgenus fits the allopatric speciation model.

Introduction

The genus *Lysipomia* Kunth comprises about forty species restricted to the Andean paramo and wet puna from 3000 to 5000 meters in elevation between 11° N and 12° S latitude. As noted by McVaugh (1955), there are two groups of species representing different "developmental or evolutionary levels" within the genus. Two of the species, *L. laciniata* and *L. sphagnophila*, are widespread and have many named, geographical subspecific taxa. One of the widespread species, *L. laciniata*, shows a disjunct distribution in the middle of its range and is absent from an area encompassing southern Ecuador and northern Peru. The remaining thirty-eight species show little or no infraspecific variation and most have extremely narrow distributions, with many endemic to a single ridge top or volcanic cone. Endemics occur throughout the Andes, but the greatest species diversity in *Lysipomia* is found between 2°-5° S latitude (18 spp.) and 6°-8° S latitude (12 spp.) on both sides of a major geologic division of the northern Andes known as the Piura Divide or the Huancabamba Depression.

This Ecuadorian/Peruvian "hot-bed" of narrow endemics directly correlates with the considerable gap seen in the distribution of *L. laciniata*. The apparent absence of one widespread species and the presence of a large number of endemic species adjacent to the Depression argue that this barrier and recent climatic changes may have played an important role in the evolutionary history of *Lysipomia*. As a result, these endemics provide us with excellent subjects with which to test the importance of such a barrier in the evolution of a genus restricted to the páramo. These tests are carried out using a hypothesis of relationship derived from a phylogenetic analysis. Phylogenetic studies of these narrow endemics are an integral first step toward understanding the biogeographical history of the Andes (Funk & Brooks 1990, Simpson & Todzia 1990). A phylogenetic context is also necessary before comparative methods can be used to answer questions of "historical ecology" such as modes of speciation and adaptive radiation (Brooks & McLennan 1991).

Taxonomic history

Within the family Campanulaceae, *Lysipomia* is unique in possessing minute capsules that dehisce via an apical operculum. This derived feature has been the key generic character since Kunth (1819) established the genus and is good evidence that the genus is monophyletic. The generic limits of *Lysipomia* have expanded over the past 150 years to include Weddell's (1857) *Rhizocephalum* (delimited by a pubescent corolla tube and an ovary that is unilocular at the apex but bilocular at the base) and Wimmer's *Dominella* (1953) (delimited by a corolla tube split on the dorsal side as in the genus *Lobelia* and the lack of anther trichomes). Features for *Lysipomia* that are derived within the family Campanulaceae include unilocular ovaries, and non-resupinate flowers. These are not unique in the family but as a unique set of characters serve to delimit *Lysipomia*.

The only detailed revision for the entire genus was prepared by McVaugh (1955). His treatment was based entirely on herbarium specimens and many species were known to him only from the type collection. McVaugh's infrageneric treatment differs significantly from Wimmer's (1953) brief revision with respect to placement of the widespread species. McVaugh used acaulescent habit and thick, fleshy roots arising from a corm-like stem to separate *L. laciniata*, one of the two widespread species, and *L. pumila* from the rest of the species. These two species constituted his subgenus *Rhizocephalum*. The other widespread species, *L. sphagnophila*, was related to all of the narrow endemics in subgenus *Lysipomia*. Wimmer placed *L. laciniata* and *L. pumila* in different subgenera based on floral morphology and related *L. laciniata* (corolla long, tubular with anthers adnate to the base of the tube) to two of the narrow endemics, *L. laricina* and *L. rhizomata*, even though they differ markedly in all other respects.

Lysipomia species possess a suite of vegetative characters not seen in temperate, montane members of the family Campanulaceae. In many species, the overall morphology appears similar to the "pachycaul" species of East Africa (Hedberg & Hedberg 1979; Mabberley 1975) although on a much smaller scale. Their stems are often very thick with extremely short internodes and all are clothed with the overlapping remains of leaf-bases. As noted above, the only truly acaulescent species are *L. laciniata* and *L. pumila*. The remaining species possess stems that are either simple and erect or dichotomously branching and prostrate.

Biogeography of the Andean Cordillera

Most workers agree that appropriate habitat throughout the northern Andes for high elevation, minute, caespitose herbs did not exist prior to 2-6 million years ago (van der Hammen 1974; van der Hammen & Cleef 1986, van der Hammen et al. 1973, Sauer 1971). Although the tectonic events (i.e., the subduction of the Nazca Plate by the South American Plate) that gave rise to the northern Andes began in the upper Cretaceous (James 1971, Zeil 1979), most of the land masses above 2000 meters have been established only since the late Tertiary, approximately 12 million years ago (Kroonenberg et al. 1990). The Andean structural units (the Central Andes of Colombia-Eastern Andes of Ecuador and the Cordillera Occidental and Oriental of Peru) that exceeded 3000 meters in the early Pliocene represent the first available high elevation habitats (Simpson 1975) and correlate with the areas of highest endemism in *Lysipomia*.

By the Pleistocene, habitats above 3000 meters were present along the entire Andean Cordillera (van der Hammen and Cleef 1986). This final uplift was concurrent with the fluctuating climatic changes associated with Pleistocene glacial events. In Colombia, van der Hammen et al. (1973) have demonstrated that glacial episodes may have lowered vegetation zones as much as 1500 meters, greatly decreasing the distance between adjacent regions of páramo or possibly creating a narrow continuous strip. Some palynological data suggests that during glacial events vegetation zones were compressed into very thin bands or vegetation from different zones was mixed, which would explain the apparent paradox of warm dry lowlands and cool wet uplands (Colinvaux 1996). These narrow bands of paramo alternated with "islands" of disjunct paramo formed during warm, moist interglacials. The fluctuating climatic changes of the Pleistocene coupled with montane topography created disjunct habitats that are thought to have lead to explosive speciation in Andean South America (Prance 1982). The formation of páramo endemics may have occurred in a manner analogous to the way in which plants colonize oceanic islands via dispersal and extinction (Vuilleumier 1970, Vuilleumier & Simberloff 1980) or speciation may be related to recolonization following glacial events (review in Simpson 1975).

Exceptions to the possibly thin but continuous bands of paramo during some glacial events could have occurred in conjunction with inadequate precipitation or the presence of a major barrier (Simpson 1975, 1979b). In the north-central Andes, one such barrier is the Huancabamba Depression. The Depression is denoted by a break in the topography such that areas above 3000 meters are dissected by deep river valleys that drain to the east (Río Huancabamba) and west (Río Piura). Although it has been suggested by some workers that sediments in the eastern Amazonian basin suggest that the Amazon originally flowed west, possibly into the Gulf of Guyaquil (Beurlen 1970, Almeida 1975), most now agree that the sediments indicate the formation of a basin for some period of time and not a mouth to the Pacific Ocean (Rasanen et al. 1987, reviewed in Kroonenberg et al. 1990). The topographic discontinuity in this area is probably much older and may reflect fault lines from the subduction of the Nazca Plate and the boundary of the Sub-Andean Front Fault Zone of the Andean Block (Ego et al. 1996). However, no adequate explanation is yet available to explain why the continuous high elevation landmasses disappear.

The Huancabamba Depression has been well recognized as a barrier to the movement of high elevation taxa and has been noted as the limit of distribution for many organisms (Vuilleumier, 1969; Simpson 1975, 1979a). During interglacials, adjacent habitats above 3000 meters on each side of the Depression are separated by at least 50 km. Recent fieldwork by Dr. Sánchez Vega and the author on the north side of the Depression indicates that the effective separation of *Lysipomia* species is much greater than 50 km because the areas above 3000 meters closest to the depression are much too dry to support most páramo species. No paleobotanical studies have documented whether paramo was ever continuous across the Depression. In *Lysipomia*, 23 endemic species are found adjacent to the Depression, 12 above and 11 below (Fig. 1). This concentration of endemics may be the product of recent climatic fluctuations coupled with the presence of a formidable geologic barrier.

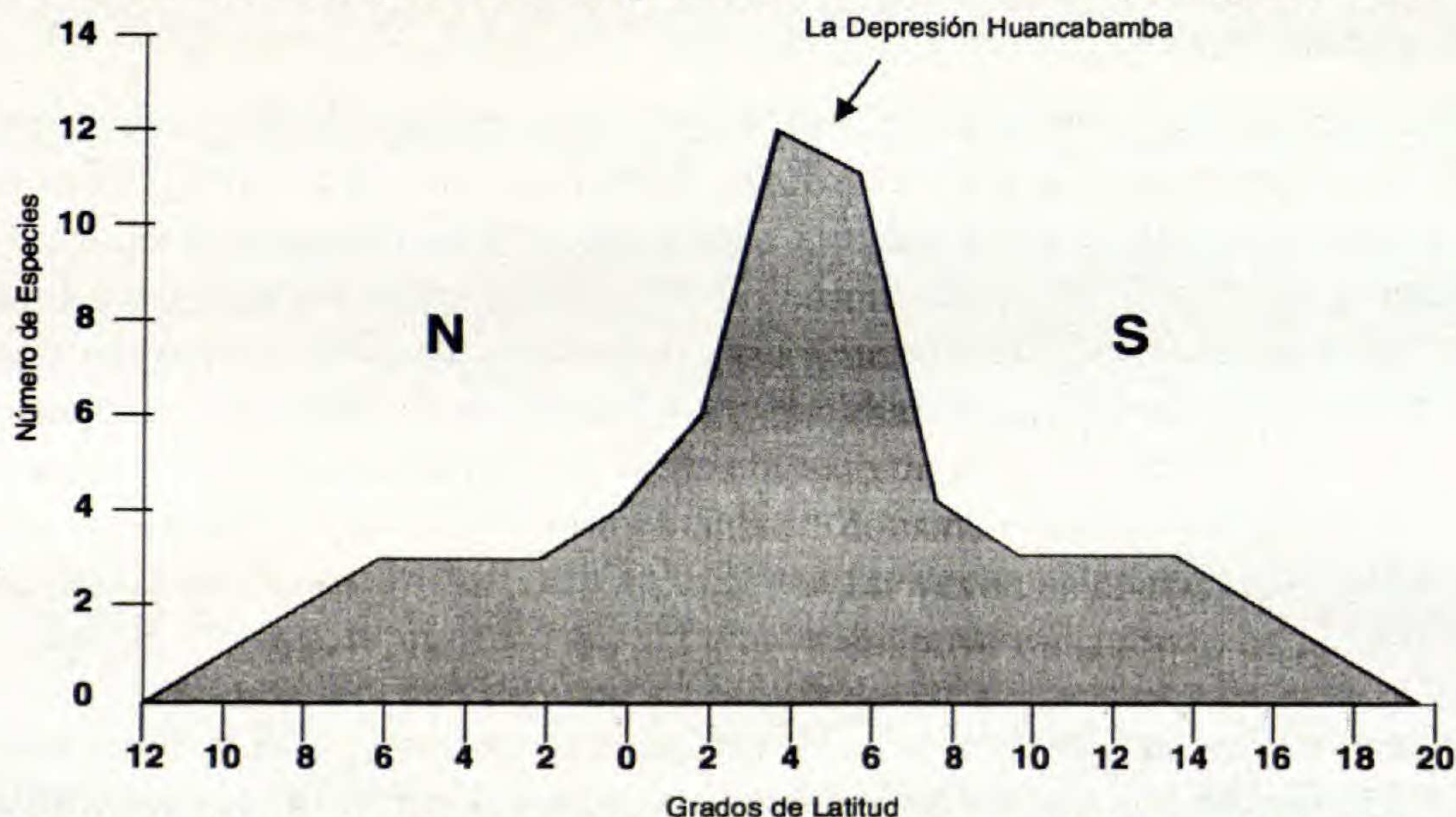


Figure 1. Graph of the number of species that occur within one degree north or south of each even latitude.

The importance of the Huancabamba Depression has been hypothesized in the evolution of endemics in other groups (e.g., Simpson 1979a, 1986; Cannatella 1982; Hart 1985; Molau 1988; Duellman & Trueb 1988). Of these studies only Hart (1985) presents an explicit phylogenetic hypothesis for a genus based on cladistic methods. Although the relationship amongst the endemics is not well resolved, Hart (1985) suggests that through peripheral isolation, endemics in *Lepechinia* Willd. have evolved from the widespread species. None of these studies dealt with an organism restricted to paramo, nor did they attempt to elucidate relationships among taxa found above and below the Depression. As noted by Cannatella, if the species on at least one side of the Depression are more closely related to each other than to those on the other side, then one can argue that the Pleistocene climatic changes in conjunction with the presence of this barrier acted as vicariant events.

This study details, for the first time, the biography of *Lysipomia* by using cladistic analyses of morphology and nuclear DNA to hypothesize species relationships. Area cladograms produced by substituting the taxon names for the areas where the species occur allow us to hypothesize the origin and radiation of this high elevation endemic. These hypotheses were then used to ask the following questions:

- Are either of the widespread species basal to clades of narrow endemics or are they highly derived?
- What is the probable origin of the genus based on the location of the least derived species?
- Has the Huancabamba Depression functioned as a “revolving door” or has the movement of species primarily been in one direction?

Materials and methods

The raw material necessary for any investigation into historical biogeography is a well-supported phylogeny (Humphries & Parenti 1986, Funk & Brooks 1990, Brooks & McLennan 1991). This study uses phylogenetic analyses based upon DNA sequence data, morphology, and anatomy of *Lysipomia*. Only 30 of the 40 species are included in this preliminary biogeographic analysis. The remaining 10 taxa are not included at the present time, because no sequence or anatomical data are available for them and the number of unknown characters are so numerous that correct placement within the cladogram would be unlikely based on morphology alone, especially because many vegetative morphological characters appear to have evolved independently in different lineages (Ayers, in prep). Due to the fact that all of the known species are not included, this biogeographic analysis must be considered preliminary and sister species relationships should be viewed as speculative. However, an analysis using 75% of the species will allow general hypotheses of origin and adaptive radiation to be formulated.

The morphological and anatomical data sets are detailed in a monograph of *Lysipomia* (Ayers, in prep.). The nuclear ribosomal sequence data (Dotti and Ayers, in press) was transformed into a numerical data set. The sequence data was then appended to the morphological and anatomical data. Transformations were performed using Winclada (Nixon, 1999) and cladistic analyses were run using Nona (Goloboff, 1994). Wagner trees were generated based upon randomized taxon order, then branch swapped. All of the replications run found the shortest tree, which had a length of 1230 steps and a consistency of 0.68. Four different topologies were generated that each had the same number of steps. The only differences in these trees was in the placement of *L. caespitosa* Ayers and all topologies were equivalent with respect to the biogeographic hypotheses presented below. Only one is included here (Fig. 2).

Results and discussion

Based upon the topology of the tree shown in Figure 2, the genus *Lysipomia* appears to be comprised of two groups or subgenera. These groups appear to be based upon floral morphology and are easily identifiable in the field by the size and color of the corolla and are designated as subgenera in the monograph in preparation. One of the widespread species, *L. laciniata*, is a basal member of the group containing the species with large corollas with nectar guides (subgenus *Rhizocephalum*). Photos of three representative species in addition to *L. laciniata* show the characteristic corolla of this group (Fig. 3). The other widespread

species, *L. sphagnophila*, is related to the other small flowered species (subgenus *Lysipomia*) that lack nectar guides (Fig. 4). Based upon statistics performed upon the DNA trees (Dotti and Ayers, in press), these two groups are well delimited and appear to have separated early in the evolutionary history of the genus.

When the localities for each taxon are substituted for their names (Fig. 5) an interesting pattern emerges within the group containing *Lysipomia laciniata* (subgenus *Rhizocephalum*). The basal members of this group are all found south of the Huancabamba Depression. Indeed, *L. laciniata*, *L. pumila*, and *L. glandulifera* are all found in southern Peru and Bolivia at the southern latitudinal limit of distribution for the genus. This distribution for most of the basal members suggests that the origin of this subgenus (and perhaps the entire genus) was in the puna, not the páramo or jalca vegetation types where most of the species now occur. The large number of more derived species found north of the Huancabamba Depression argues that adaptive radiation has been from south to north. Because there is only one species pair that are separated by the Depression (*L. speciosa* and *L. brachysiphonia*), the Huancabamba Depression appears to have been a significant barrier that the taxa in this subgenus have not been able to cross and movement appears to be in one direction only, from south to north. Independent population level analyses of *L. laciniata* (Dotti and Ayers, submitted) confirm that most of the genetic variation within that species is found in the southern part of its range and that the populations in Colombia show little genetic variation. This suggests that the occurrence north of central Peru may be due to a single dispersal event or a few independent dispersal events (Dotti and Ayers, submitted).

The remainder of the subgenus *Rhizocephalum* appears to be limited to the northern Andes with most species occurring in southern Ecuador. Species richness in the derived clades increases with proximity to the northern side of the Huancabamba Depression. Two species (*L. sparrei* and *L. crassomarginata*) known only from extreme southern Ecuador were collected by Dr. Sánchez Vega accompanied by the author in May 1997 near Laguna Shimbe just north of the village of Huancabamba. Two additional species (*L. biliniata* and *Lysipomia* sp. indet. Sánchez Vega 8854) may also be new reports for Peru. These were not seen growing wild but had been gathered as medicinal plants by a local merchant. The addition of four species of *Lysipomia* to the flora of Peru during this short (one day) field expedition to the paramo north of the Huancabamba Depression suggests that this area is undercollected and may support a rich flora undocumented for Peru.

Documentation of the co-occurrence of sister species (although preliminary at this time) could also undermine the generally supported allopatric speciation model. The ridgelines and mountain tops just to the north of the Huancabamba Depression harbor groups of species that appear to be each others closest relatives and in some areas such as the Lagunas de Compadre south of Loja, Ecuador (Espinosa 1948, Ayers in prep), or Cerro Toledo south of Yangana, Ecuador (Ayers in prep), these species appear to be growing adjacent to each other in seemingly identical habitat. Although sister species might have migrated into areas of sympatry and suffered extinction in their original localities, migration is unlikely given the lack of easily dispersed seeds or some means of vegetative reproduction in these species. Migration may also have been impossible due to the lack of intervening suitable habitat caused by the lack of continuous areas at 2000-3500 meters in elevation. A complete cladistic

analysis of these sympatric sister taxa coupled with a better understanding of Pleistocene climatic fluctuations could provide tests for the mode of speciation.

The second group, subgenus *Lysipomia*, containing all of the small-flowered species, is slightly less species rich than the other subgenus, but because of the four new species recently collected by Dr. Sánchez Vega in northern Peru coupled with their small size, they may not be well collected. It stands to reason that many more species await discovery in the mountains of northern Peru. Unlike the large-flowered group, the subgenus *Lysipomia* does not show an obvious trend in its adaptive radiation with respect to the Huancabamba Depression. Nor does the widespread species, *L. sphagnophila*, appear to be basal within the lineage. Three species in this subgenus occur on both sides of the Huancabamba Depression (*L. sphagnophila*, *L. montioides*, *L. multiflora*) compared to only one species, *L. laciniata*, in the large-flowered subgenus *Rhizocephalum* discussed above. Because two of the three basal species and three-quarters of all of the species occur south of the Depression, the origin of the subgenus may have been in the mountains south of the Huancabamba Depression. Unlike the subgenus *Rhizocephalum*, the members of subgenus *Lysipomia* do not occur in the extreme southern portions of Peru or in Bolivia. The corolla morphology seen in *Lysipomia* may correlate with their breeding system, the small-flower species being self-compatible (Ayers, in prep.). In a growth chamber at Northern Arizona University, many species within the small-flowered subgenus have been reared from seeds collected in the field. Without exception, all flower profusely and set seed without hand pollination. Self-compatibility may allow even a single seed to potentially establish a new population.

There is one pair of sister species in the small-flowered subgenus *Lysipomia* (*L. muscoides* and *L. delicatula*) that are separated by the Huancabamba Depression. The pair had been considered to be geographical varieties of a single species (McVaugh, 1955) until collections made in 1996 and 1997 by Dr. Sánchez Vega allowed complete morphological examination. The possible progenitor or parent species, *L. muscoides*, is widespread in Colombia and northern Ecuador with a single collection from Merida, Venezuela. Only one population of *L. delicatula* has been found growing on the eastern slopes of Cerro Calla Calla above Leimebamba, Amazonas, Peru. The Río Marañón has also been an effective barrier in this subgenus. Two sister species, *L. hutchinsonii* and *L. sp.nov. Sánchez Vega 8869* grow on opposite sides of the river on Cerro Calla Calla and at Kumulca, west of the town of Celendín.

Although there are some localities where three species from subgenus *Lysipomia* grow sympatrically (e.g., Las Lagunas, Km 50 north of Cajamarca), there are no areas where sister species within the small-flowered subgenus *Lysipomia* co-occur. This distribution would fit the allopatric speciation model generally held to be the more common mode of speciation (Grant, 1981).

Although these results do not include all of the taxa, the general patterns should provide insight into the probably origin and adaptive radiation with *Lysipomia*. Whereas the biogeographic patterns seen in the two subgenera of *Lysipomia* are quite different, they share centers of diversity and their probable origin is south of the Huancabamba Depression in central or southern Peru. The apparent species richness adjacent to the Huancabamba

Depression can only be explained by the discontinuous terrain above 3000 meters coupled with Pleistocene climatic fluctuations. Compression of vegetation from different communities into discreet narrow bands or areas with mixed vegetation from disparate communities would have placed severe selection pressure on minute alpine tundra plants. Field work supports the hypothesis that even small amounts of competition from grasses, ferns, or shrubs effectively eliminates the occurrence of *Lysipomia* species. In such habitats, *Lysipomia* is often limited to disturbed areas caused by erosion or adjacent to senderos. The few species that occur below 3000 meters are found only on extremely windy, barren, rocky outcrops (Ayers, in prep.). Further refinement on this data and inclusion of all of the species will allow finer resolution of the sister relationships and the areas where endemic occur. Further phylogenetic analyses will be required to decipher which lobelioids are the closest relatives of this high elevation genus and whether they originated from neotropical lobelioids or whether the migration of a holarctic ancestor preceded the origin of *Lysipomia*.

Because of the patterns of species richness seen in *Lysipomia*, increased field work in northern Peru on both sides of the Huancabamba Depression is urgently needed to catalogue the flora in this potential "hot-spot" of diversity. Species richness has been documented for the moist forests of northern Peru (Dillon, 1994) but few surveys have been done of the páramo and jalca. Although a survey of a single areas above 3000 meters would not appear to be particularly species rich, endemism is high and when many adjacent areas are combined they approach the species richness found in montane forests of the eastern Amazon (Gentry, 1993). Within *Lysipomia* almost half of the previously known species (14 of 30) and all of the undescribed or recently described species (Ayers, 1997), occur between 2° and 8° South Latitude. If the species richness seen in *Lysipomia* can be used as an indicator of diversity, then the high elevations on both sides of the Huancabamba Depression should be a priority for floristic surveys and monographers.

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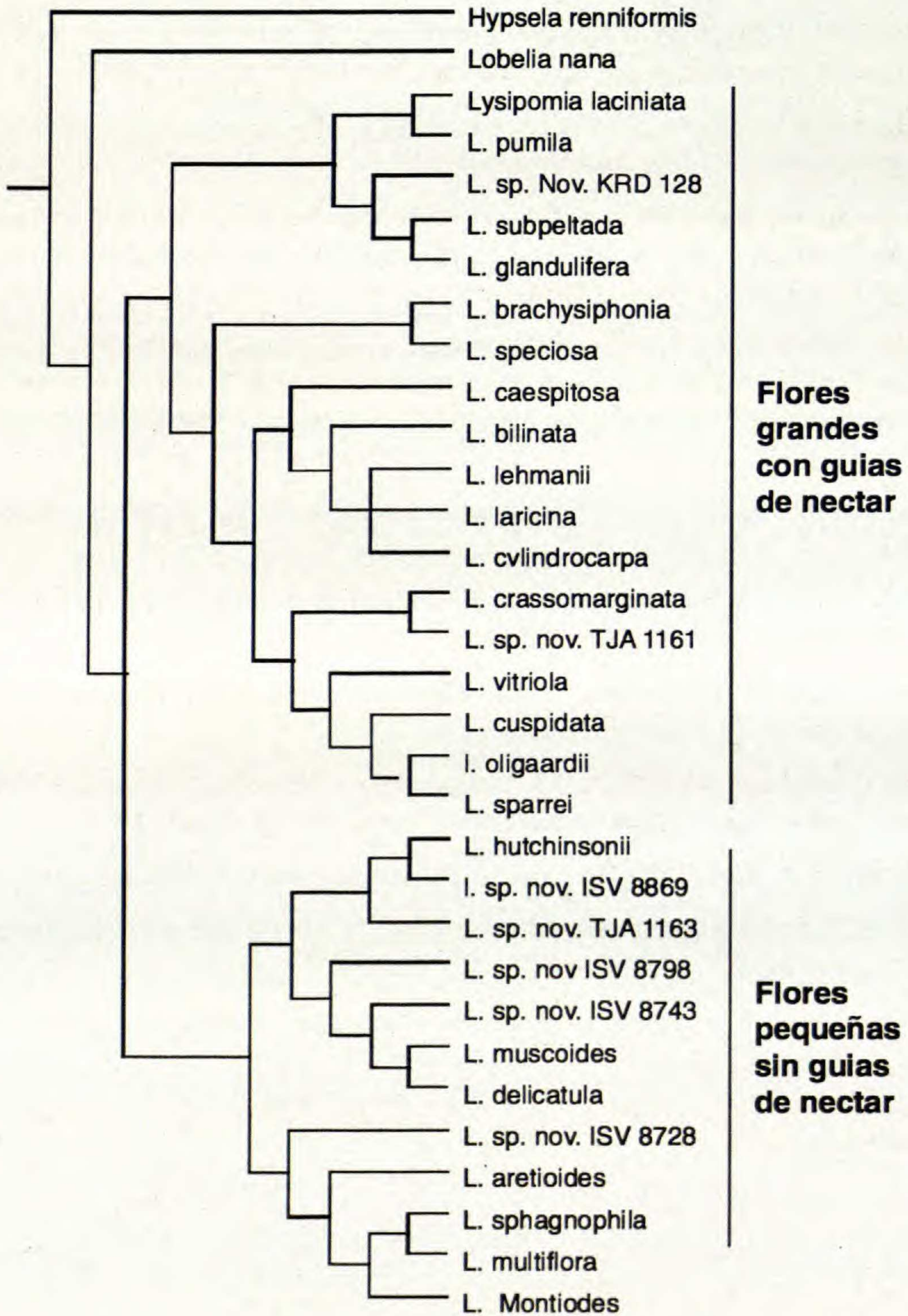


Figure 2. The two subgenera in *Lysipomia* depicted on one of four cladograms produced from a combined data set containing nrITS DNA sequence data, morphology, and anatomy. Length 1230 steps; consistency 0.68.



Figure 3. Four representatives of *Lysipomia* subgenus *Rhizocephalum*; (A) *L. laciniata* (Ayers 1201); (B) *L. biliniata* (Ayers 1427); (C) *L. subpeltata* (Sánchez Vega 8885); (D) *L. glandulifera* (Sánchez Vega 8870).



Figure 4. Four representatives of *Lysipomia* subgenus *Lysipomia*; (A) *L. sphagnophila* (Sánchez Vega 8845); (B) *L. sp. nov.* (Sánchez Vega 8809); (C) *L.sp. nov.* (Sánchez Vega 8869); (D) *L. hutchinsonii* (Sánchez Vega 8895).

